Jackson, R. R. and C. E. Griswold, 1979. Nest associates of *Phidippus johnsoni* (Araneae: Salticidae). J. Arachnol. 7:59-67.

NEST ASSOCIATES OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE)

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ABSTRACT

Spiders (Gnaphosidae, Clubionidae, etc.), insects (Collembola, Lepidoptera, etc.), and other invertebrates (mites, isopods, millipedes, and snails) were found inside, on, under, and beside nests of *P. johnsoni*. Some nest associates were found at nests that were occupied by *P. johnsoni* at the time, but most were at unoccupied nests. Dead organisms, in some cases possibly prey remains of *P. johnsoni*, and exuvia of other organisms were found also. Hypotheses concerning the adaptive significance of associations are discussed, including predation on *P. johnsoni* and their eggs, scavenging, and the use of *P. johnsoni* nests as shelters.

INTRODUCTION

Adaptive radiation in spiders has led to a great diversity of adaptations related to the use of silk. In many cases, structures such as webs, egg cases, and nests are constructed by the spider and remain in the environment for some time afterwards. These may be involved in functions related to prey capture, protection from predators, communication, and other aspects of the spider's biology. However, use of these structures is not restricted to the individual or the species that constructed them, since other organisms may form various types of associations with the silken constructions of spiders. This paper will consider organisms that associate with the nests of the salticid spider *Phidippus johnsoni* Peckham and Peckham.

Vagabond spiders such as the salticids do not build prey capturing devices from silk. However, many build nests (retreats) in which they may molt, mate, oviposit, and remain when inactive. Although associates of the web-building spiders have attracted considerable interest, associates of the nests of vagabond spiders have recieved relatively little attention.

Some species of spiders are apparently specialized as predators of web-building spiders in their webs, and these are frequently found in the webs of their prey (Bristowe 1958, Czajka 1963). Other species are "kleptoparasites" (Bristowe 1958, Legendre 1960, Vollrath 1976). Sometimes the webs of one species of spider have lines fastened to webs

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of another species. Also, one may find one species inside an occupied web of another species, as an occasional rather than a routine occurrence, and predation on insects in the host's web or on the host itself may occur (Bentzien 1973, Bristowe 1958, Crocker and Felton 1972, McCook 1889, Roberts 1969). Various insects are sometimes found in the webs of spiders, in which they may feed on prey caught in the web or prey remains left by the host; or they may be predators or parasites of the spider or her eggs (Bristowe 1941, China and Myers 1929). Various salticid species will enter both occupied and unoccupied webs of other spiders, sometimes building their nests there, and sometimes preying on the host (Bristowe 1941, Jackson 1976, McCook 1889, Nielsen 1931, Robinson and Valerio 1977, Tolbert 1975). Various insects and foreign spider species live in the webs of "social" spiders (Brach 1977, Diguet 1915, New 1974), and generally the adaptive significance of these associations are poorly understood.

The data in this paper were collected in conjunction with studies of the reproductive biology and life history of this species (Jackson 1976a, 1978a, b). During the course of these studies it was possible to become quite familiar with the shape, size, and texture of *P. johnsoni* nests and to distinguish them from those of other common sympatric vagabond spiders that use the same nest sites, primarily gnaphosids and clubionids. It became apparent that other species are frequently inside nests built by *P. johnsoni*, and data were collected concerning these. Since this species occurs at rather high densities in the field (2 to 30 per 1000 sq. m.; Jackson 1978a), both occupied and unoccupied nests of *P. johnsoni* would seem to be potentially important physical features in these habitats, making the associates of this species of special interest.

METHODS AND MATERIALS

The species involved in this study was determined as *P. johnsoni* from descriptions provided by Peckham and Peckham (1900, 1909) and from labeled museum specimens, including ones identified by the Peckhams. The spiders that Peckham and Peckham (1909) identified as *P. formosus* are apparently the same species as *P. johnsoni* (Jackson, unpublished data). Kaston (1972) noted this also. Spiders of the *formosus* form are found especially in southern California. In this study, spiders from Santa Barbara and Palomar were primarily ones of the *formosus* form. In the remaining populations, the *johnsoni* form predominated.

Whenever an organism other than *P. johnsoni* was found inside, underneath (between the nest and the rock, piece of wood, etc.), on (touching the nest but not underneath), or beside (within a few millimeters of the nest) the nest, it was collected, if possible, and notes were made concerning the nest and its contents. The primary habitats from which these data came were the census areas (Jackson, 1978a), similar neighboring areas, plus several additional habitats not previously described. Each study site will be briefly characterized here, with information given in the following order: location, elevation (recorded as nearest 500 m), plant community, description, primary nest sites (in parentheses). The classification system of Munz (1959) is used for California plant communities.

A. Tilden–Coastal Range (California, Contra Costa Co.). 500m. Coastal Prairie. Rocky, grass covered slopes (rocks).

B. Mt. Diablo–Coastal Range (California, Contra Costa Co.). 1000m. Foothill Woodland. Rocky, grass covered slopes (rocks).

C. Santa Barbara–Coastal Range (California, Santa Barbara Co.). Santa Ynez Mountains. 500m. Valley Grassland. Rocky, grass covered slopes (rocks).
D. Palomar Mountain–Transverse Ranges (California, San Diego Co.). 1500m. Southern Oak Woodland. Rocky, grass covered slopes (rocks.)
E. Point Reyes–Beach (California, Marin Co.). Sea level. Coastal Strand. Sand dunes near ocean (wood on ground).
F. Inglenook–Beach (California, Mendocino Co.). Sea leavel. Coastal Prairie and Coastal Strand. Sand dunes and bluff near ocean (wood on ground, fence posts, dead trees).
G. Pothole Dome–Alpine (California, Mariposa Co.). Sierra Nevada. 2500m. Lodgepole Forest. Open, rocky areas on granite dome (rocks).
H. Tenaya Lake–Alpine (California, Mariposa Co.). Sierra Nevada. 2500m. Lodgepole Forest. Open, rocky areas on granite dome (rocks).
I. Whiskey Mountain–Alpine (Wyoming, Fremont Co.). Rocky Mountains. 3000m. Timberline. Extremely rocky slopes (rocks).
J. Blacktail Butte–Subalpine (Wyoming, Teton Co.). Rocky Mountains. 2000m. Conifer forest. Open, rocky areas within forest (rocks).

RESULTS AND DISCUSSION

Many spiders (77) were found associated with nests of *P. johnsoni* (Table 1). Of these, 61 percent were gnaphosids. Sixty spiders, including 42 gnaphosids, were inside *P. johnsoni* nests; insects (17) and other invertebrates (7) were found less frequently. These seem to be less prone to be inside the nests, since only nine insects and two other invertebrates were found inside nests. In addition, dead organisms and exuvia were sometimes found associated with *P. johnsoni* nests. Except for springtails, mites, and ants, only one living individual nest associate was found at any given nest, although a *P. johnsoni* might be present at the same nest with the associate.

An estimate for the proportion of the total number of nests occupied by nest associates was obtained from monthly censuses at Tilden, Mt. Diablo, Pt. Reyes, and Inglenook (Jackson, 1978a), pooling data for all months and all habitats. Also, for this subset of the data, only those organisms actually inside nests were considered. Of the 4,137 *P. johnsoni* nests encountered, 69% were occupied by *P. johnsoni* at the time. Nest associates were not found in any of the nests containing *P. johnsoni* during the censuses, but they were found inside 4.1 percent of the remaining nests, or 1.3 percent of the total number of nests encountered. The potential nest-associated predator of *P. johnsoni*, *Herpyllus hesperolus* Chamberlin (Jackson 1976b), was found inside two of the *P. johnsoni* nests in these censuses.

Any nests for which there was doubt concerning the species by which it was built were not counted. Consequently, estimates are conservative. There are no apparent differences in the empty versus occupied nest ratios in the different habitats or for different habitats or for different times of the year.

Springtails And Mites–Two very common types of nest associates are not listed in Table 1, springtails and mites (Anystidae). These small arthropods were frequently seen in, on, under, or beside nests, especially ones not occupied by *P. johnsoni*, but also ones that were still occupied. Often they were associated with nests containing other nest associate species, exuvia, eggshells, or other contents. The mites and springtails sometimes occurred at the same nests together. Sometimes the bright red anystid mites were present

Table 1.—Living organisms found associated with nests of *Phidippus johnsoni*. Except when otherwise stated, the associate is mature. For associates not identified to species, the lowest taxonomic determination is given. Numbers refer to the total number of nests occupied by the indicated associate; parenthetical breakdown refers to numbers found inside the nest, under the nest, on the nest, and beside the nest, respectively. Letters refer to habitats in which a given associate was found (see Methods and Materials).

ASSOCIATES	NUMBER	HABITATS
Araneae		
Gnaphosidae		
Zelotes sp.	34 (31, 1, 1, 1)	A, B, E, F, G
Herpyllus hesperolus Chamberlin	7 (5, 0, 0, 2)	A, B
Drassodes neglectus Keyserling	2 (2, 0, 0, 0)	I
Gnaphosa muscorum C. L. Koch	1 (1, 0, 0, 0)	I
Gnaphosa brumalis Thorell	1 (1, 0, 0, 0)	I
Haplodrassus sp.	1 (1, 0, 0, 0)	D
Undetermined genus	1 (1, 0, 0, 0)	C
Clubionidae		
Clubiona californica Fox	7 (7, 0, 0, 0)	E, F
Clubiona sp. 1	5 (5, 0, 0, 0)	A, B
Clubiona sp. 2	1 (1, 0, 0, 0)	H
Scotinella sp.	2 (1, 1, 0, 0)	A
Agelenidae		
Calilena restricta Chamberlin and Ivie	5 (0, 0, 0, 5)	B
Dictynidae		
Dictyna sp.	2 (1, 1, 0, 0)	F
Erigoniidae		
Undetermined genus	2 (1, 1, 0, 0)	B, F
Salticidae		
Talavera minuta Banks	2 (1, 1, 0, 0)	A
Thomisidae		
sp. 1	2 (1, 0, 1, 0)	F
sp. 2	1 (0, 0, 1, 0)	A
Amaurobiidae		
Titanoeca sylvicola Chamberlin and Ivie	1 (0, 1, 0, 0)	I
Lycosidae		
Pardosa sp.	1 (1, 0, 0, 0)	F
Insecta		
Lepidoptera		
Unidentified larvae	4 (4, 0, 0, 0)	A, B
Unidentified pupa	1 (0, 0, 1, 0)	A
Dermaptera	4 (3, 1, 0, 0)	A, F
Hymenoptera		
Formicidae	3 (1, 0, 2, 0)	F, J
Coleoptera		
Elateridae	2 (0, 2, 0, 0)	F, I
Staphylinidae	1 (1, 0, 0, 0)	B
Thysanura		
Lepismatidae	1 (0, 1, 0, 0)	F
Crustacea		
Isopoda		
Armadillidium vulgare Latreille	4 (2, 1, 1, 0)	E, F
Diplopoda	1 (0, 1, 0, 0)	F
Gastropoda	2 (0, 0, 2, 0)	F

in numbers in excess of 30 at nests not occupied by *P. johnsoni*. When, as often occurred, smaller numbers of mites or springtails were present, they were not so conspicuous and careful searching was necessary in order to discover them. In general, records were not kept of these arthropods.

Vagabond Spiders–Of the spiders listed in Table 1, salticids, gnaphosids, clubionids, thomisids, and lycosids are vagabond species. For molting and oviposition, and in some species during periods of inactivity in general, these spiders go inside nests that they construct from silk. These are usually tubular structures, not so unlike those of *P. johnsoni* in their general form. Many of the observations of individuals from these groups occupying *P. johnsoni* nests may have been cases of the spider simply making use of an available nest that it did not itself construct. The adaptive significance of this could be related to avoiding the expenditure of time and energy that would have been necessary in order to construct a nest of its own. Also, a nest of *P. johnsoni* might be preferable in some ways to nests the associate could construct. For example, the nests of *P. johnsoni* tend to be rather large and densely woven with silk (Jackson 1978b). In comparison, the nests built in the laboratory by *H. hesperolus*, *Zelotes*, and the unidentified *Clubiona* from Tilden are not very densely woven, and the nests these spiders were found occupying in the field when not inside *P. johnsoni* nests were relatively filimsy in appearance. The larger, more dense nests of *P. johnsoni* might provide greater protection from predators, parasites, dessication, or other perils for these spiders than the nests they construct themselves.

The salticid *Talavera minuta* Banks warrants special mention. Adults of this species are much smaller in body size than *P. johnsoni*. The one found under a *P johnsoni* nest was inside a nest of its own, which differed in appearance and was much smaller than *P. johnsoni* nests. A few other individuals of this species were found at Tilden in similar nests, under rocks. In the case of the *T. minuta* found inside a *P. johnsoni* nest, this nest was considerably larger than the spider.

In the case of the *Drassodes neglectus* Keyserling and one of the unidentified *Clubiona* from Tilden, an exuvium was in the nest with the spider. These exuvia presumably came from the nest associates, since size and eye arrangement were appropriate for the associates in each case. On two occasions at Mt. Diablo, a large gnaphosid exuvium, probably of *H. hesperolus*, was found in a nest not containing spiders. Twice, an exuvium of a gnaphosid (one, probably of a *Zelotes*; the other, probably of a *Herpyllus*) was found in a *P. johnsoni* nest with a *P. johnsoni* exuvium. The following gnaphosids were found inside *P. johnsoni* nests with *P. johnsoni* exuvia: *Zelotes*, 4; *Herpyllus hesperolus*, 1; *Haplodrassus* 1; and *Gnaphosa muscorum* C. L. Koch, 1. Clearly, spiders occupy nests that they do not themselves construct. Whether or not spiders that occupy the nests of other spiders spin inside them or otherwise alter them is not known.

One of the *Zelotes* was found inside a *P. johnsoni* nest with dried *P. johnsoni* eggs, and possibly these were eaten by the gnaphosid. There was a living immature *P. johnsoni* inside the nest on which the *Scotinella* sp. was found.

Gnaphosids As Predators–Except for *Zelotes*, the gnaphosids in Table 1 were of size comparable to or larger than the adults of *P. johnsoni*. The two individuals of *Drassodes neglectus* were found inside nests containing dead *P. johnsoni*, which had probably been killed and eaten by the gnaphosids. In the case of one of the two *H. hesperolus* found beside a nest, there was an immature *P. johnsoni* inside. The other *H. hesperolus* was inside a nest resembling those that this species constructs itself, fastened at one end to an empty *P. johnsoni* nest. In the case of one of the *H. hesperolus* inside a nest, an immature

P. johnsoni was standing beside the nest. Laboratory experiments indicated that *H. hesperolus* will prey upon *P. johnsoni* that they find in nests. Males of *P. johnsoni* have alternative forms of courtship (Jackson 1977a), one of which is vibratory in nature and performed on the nests of females. In the laboratory, *H. hesperolus* sometimes prey upon males that court at nests constructed by *P. johnsoni* females but occupied by the gnaphosids (Jackson 1976b). Similar predation might occur on females and immatures of *P. johnsoni*, when they depart then return to the same nest or enter nests built by other conspecifics (Jackson 1978b). Further study is needed in order to ascertain the importance of this type of predation as a selection factor favoring gnaphosids associating with *P. johnsoni* nest.

Web-Building Spiders—Amaurobiids and dictynids are web-building spiders, but there were no webs in the vicinity of the individuals found associated with *P. johnsoni* nests. Probably they were simply taking temporary shelter at the nests.

Each agelenid found beside a *P. johnsoni* nest was in a web that was attached to and partially covered the *P. johnsoni* nest. In each case, a live *P. johnsoni* was inside the nest. More information is needed before much can be concluded concerning the relationship between the agelenids and the salticids in these instances. Perhaps the web touches the nest purely by chance, as a result of being built under the same rock. Although salticids are known to place their nests near or in webs of other spiders (McCook 1889), this seems less likely in these cases because the agelenid webs partially covered the salticids nests, rather than vice versa, suggesting that the webs were built after the nests. Perhaps the silk nests are particularly sturdy or easily employed attachment sites for webs compared to the rock or vegetation.

Other Invertebrates—The nests of *P. johnsoni* may be convenient, suitable shelters for various organisms besides spiders, perhaps largely accounting for many of the insects and other invertebrates found inside and under nests (Table 1).

Concerning the lepidopteran larvae inside *P. johnsoni* nests and the pupa on a nest, perhaps the nests of *P. johnsoni* provide an especially suitable site for some lepidopterans to construct their cocoons when they pupate. Possibly these lepidopterans augment the silk that they produce with the existing silk of the nest.

Each of the two nests at which ants were found at Blacktail Butte contained dead *P. johnsoni* (one, a male; the other, a female plus eggs). Approximately five of these small black ants were found at each nest. They were on the outside only of the nest containing a dead female; but both outside and inside the nest containing the male. It would seem probable that ants feed on dead *P. johnsoni* and possibly their eggs when they find them. Considering the small size of the ants, the possibility that they kill *P. johnsoni* before feeding seems less likely. At Inglenook a single small black ant was found on a nest occupied by a female *P. johnsoni*. Possibly various organisms are prone to enter *P. johnsoni* nests and feed on dead *P. johnsoni* or their eggs, but more information is needed concerning this. In the laboratory, *P. johnsoni* that spontaneously died were sometimes inside their nests when found (Jackson 1978a).

An exuvium of an earwig was found on an empty nest, and another was found inside a nest occupied by an immature *P. johnsoni* plus a *P. johnsoni* exuvium.

Dead Organisms—Dead organisms were sometimes found on the surface of *P. johnsoni* nests. A small gastropod shell at Tilden and a dead millipede at Inglenook were probably fortuitous events. Other cases may have been remains of prey left by *P. johnsoni* at their nests. *P. johnsoni* have been seen in the field and the laboratory standing beside their nests while feeding. Three *Pardosa* (Lycosidae), seven large flies, one honeybee worker

(*Apis mellifera*, Apidae), one aphid (Aphidae), and one stink bug (Pentatomidae) had the appearance of prey fed upon by *P. johnsoni* (i.e., they were dry, hollow, macerated carcasses). With the exception of the stink bug, *P. johnsoni* have been observed in nature feeding on members of each of these groups (Jackson 1977b). In some cases, *P. johnsoni* were inside the nests on which the dead organisms were found: one of the *Pardosa*, five of the flies, the honeybee, and the stink bug.

Parasitoids and Parasites—One acrocerid fly larva emerged from an immature *P. johnsoni* in its nest and pupated in the laboratory (collected at Del Puerto Canyon near Mt. Hamilton, California). The spider probably would have died in its nest if it had been in nature. The acrocerids are parasitoids on spiders (Bristowe 1941, Schlinger 1960).

Egg parasites have been reared from nests of several *Phidippus* species (Coquillet 1892, Davidson 1896, Edwards 1975), although they have not been reported so far for *P. johnsoni*.

***Phidippus Johnsoni* Inside Gnaphosid Nest**—More than 3500 *P. johnsoni* have been observed in nature inside nests. Only once was one found inside a nest clearly of another species. This was an adult male at Mt. Diablo found inside a relatively large nest that resembled closely those constructed by *H. hesperolus*. Perhaps it is significant that this was a male, since males seem to have a life style that emphasizes searching for females and mating (Jackson 1978a, b). Females and immatures may be more sedentary. A nomadic male might be the most likely class of *P. johnsoni* to take refuge in a nest it did not itself construct, even rarely those of other species.

GENERAL DISCUSSION

Although generally this is not a phenomenon that has attracted much attention, there are sufficient reports in the literature to suggest that association between organisms of various types and the nests of vagabond spiders are fairly common. Yates (1968) and McCook (1889) reported several cases of one species being found on or inside the nests of another species. Myers (1927) noted that ladybird beetles (*Rhyobius ventralis*) sometimes occupy deserted nests of the salticid *Holoplatys senilis* Dalmas. Also they may be found inside nests occupied by the salticid simultaneously, but inside a different chamber. Lamoral (1968) studied four species of intertidal, non-salticid spiders that build nests in mollusk shells, crevices of rocks, and similar locations. One species frequently occupied nests of the other species rather than building ones of its own. Also these spiders often feed at the nest, and a springtail was found at the nests as a scavenger. China and Myers (1929) reported instances of hemipterans found in nests of oxyopid spiders.

Auten (1925) discussed organisms found associated with nests containing eggs of the vagabond spider *Philodromus canadensis* Emerton (Thomisidae) plus those of some web spiders, two Araneidae and one Theridiidae. She concluded that there were three types of associates: parasites, predators, and accidental inhabitants. The present report for the salticid *P. johnsoni* differs in a number of ways. Auten restricted her study to nests containing eggs, while our study included all nests regardless of the presence or absence of eggs or spiders. This may have accounted for some differences, such as the failure in our study to find the parasites and parasitoids of eggs and spiders Auten found (Ichneumonidae, etc.). The major group of nest associates found in this study was other spiders, a group not reported in Auten's study. The predators that she found were probably primarily predators of eggs and young spiderlings, while possible predators of adults and larger immatures were found in our study.

Considering Auten's study in conjunction with ours, classes of possible nest associates of vagabond spiders can be summarized as follows:

1. Parasites and parasitoids of spiders that seek out and/or emerge from their hosts inside nests.
2. Parasites of eggs in nests.
3. Predators of eggs and spiders in nests.
4. Scavengers feeding on dead spiders in nests.
5. Predators that adopt nests as a predatory device. This might include the gnaphosids that prey on *P. johnsoni* males that court at nests built by *P. johnsoni* females, but occupied by the gnaphosid. (Jackson 1976b).
6. Nest-building spiders that adopt nests of other species as a substitute for constructing their own nests.
7. Organisms that adopt nests as a particularly suitable refuge or pupation site. More work is needed to determine how sharp the distinction is between this category and the next one.
8. Accidental inhabitants, or ones that just happen to be in or around the nest, and for which the association has no particular significance.

ACKNOWLEDGEMENTS

David E. Hill, Frank A. Enders, Robert T. Yamamoto, and Mary Catharine Vick are gratefully acknowledged for comments on the manuscript. Thanks are extended to Evert I. Schlinger and Roy L. Caldwell for their assistance in the earlier phases of the study. Thanks go to Herbert Levi, Norman Platnick, and Robert Schick for loan of specimens. The California Department of Parks and Recreation, the East Bay Regional Park Service, and the National Park Service are gratefully acknowledged for their assistance.

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